An uplifting experience

David Rind

PROJECTIONS of a rapid warming of the climate over the next century, due to increased greenhouse gases, have focused attention on the last time the Earth experienced very warm climates, during the Tertiary Period (63–2.5 million years ago). The end of that era, and the onset of the modern alternation between glacial and interglacial climes, has been related to the rapid development of the great mountain belts, particularly the Himalaya. A recent mini-conference on *Uplift, Erosion and Climate** brought together various protagonists to argue out the cases for and against a causal connection.

The simplest story[1,2] is that the rapid development of mountains during the past 5–10 million years started the ice ages. Erosion and associated chemical weathering would have drawn carbon dioxide out of the atmosphere to start the cooling[3]. The reduced temperatures might then have slowed down the rate of weathering, so stabilizing the CO_2 level. As acknowledged by all of the participants at the meeting, many uncertainties surround the observations and their interpretation, but the debate could clearly be broken down into a number of distinct issues.

Did rapid uplift really occur? Apparently not. As emphasized by P. Molnar (Massachusetts Institute of Technology), much of the evidence suggesting rapid uplift can be explained more easily in terms of the colder climate of the Late Cenozoic[4]. A colder climate produces glaciers and alters botanical distributions, making it appear as if elevation was increasing; in the case of Tibet, tectonically driven northward movement over this time would also have produced cooling. Furthermore, with increased erosion, due either to glaciers or to greater storminess, an isostatic (buoyant) response will raise the elevation of individual peaks, giving the appearance of uplift while in fact lowering the mean elevation relative to sea level. There is no obvious tectonic reason for widespread rapid uplift in the late Cenozoic when, according to T. Volk (New York University), spreading rates had decreased. Uplift probably occurred over a longer time frame, of some 50 million years, in the Himalayan region. But there may have been some acceleration 8 million years ago associated with a sudden increase in the intensity of monsoons (W. Prell, Brown University).

High peaks in Nepal, south of Everest. Cause or effect of climate change? Or neither? (Photo by David Paterson.)

Did increased erosion occur in the later Cenozoic? Probably. Increases over the past 50 million years in the seawater $^{87}Sr/^{86}Sr$ ratio recorded by marine carbonates (D. DePaolo, University of California at Berkeley) imply an increase in the volume of continental weathering, although changes in source composition and path to the ocean are also possible. Greater physical weathering might be expected in the colder climate and with gradual uplift in southern Asia. The strontium changes are assumed to imply increases in the chemical weathering of silicate rocks, although this is harder to prove: it presupposes that there has been an increase in the volume of weathered rock, and that the strontium is not coming from carbonates. The idea that weathering slows as temperatures cool, owing to reduced reaction rates, so stabilizing the CO_2 level[5], is in general conflict with this approach, which emphasizes the importance of physical weathering in increasing the surface area available for chemical reactions.

Did CO_2 levels decrease during the Cenozoic? This is certainly the general assumption, but the evidence for it is pretty weak. Theoretical models of the long-term carbon cycle attempt to balance CO_2 sources, chiefly volcanic emissions whose change with time is estimated from sea-floor spreading rates, with sinks such as silicate weathering or organic-carbon burial (R. Berner, Yale University). Many of these parameters are not well known. Additional estimates of CO_2 levels come from the ^{13}C content of palaeosols or marine organic material, both of which appear to be affected by the prevailing gaseous CO_2 concentration. Numerous assumptions apply here as well, and the range of estimated CO_2 levels for the Tertiary varies from seven times pre-industrial levels to no difference[6]. We do not really know what CO_2 concentrations were throughout the Tertiary; recent work, in fact, suggests that values in the late Pliocene (3.2 million years ago) were no higher than they were in pre-industrial times[7] (M. Raymo, Massachusetts Institute of Technology), despite evidence indicating that polar climates were much warmer.

Were higher CO_2 levels responsible for the warm climates in the Tertiary? Again, this is the general assumption, yet there is a considerable discrepancy between the climates reconstructed from geochemical and other data for this period and those predicted from models of an atmosphere with increased CO_2. Tertiary climates as deduced from oxygen-isotope analysis and pollen data feature extreme warming at polar latitudes (of the order of 15 °C), with little temperature change in the tropics. In contrast, models for increased CO_2 produce substantial tropical warming as well, with increased water vapour levels

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providing a strong positive feedback. As reported at the meeting, our model experiments[8] can reproduce the extreme high-latitude temperature amplification of the reconstructions only by increasing ocean heat transport, a process by which sea ice becomes the prime positive feedback. The increased ocean heat transport might have come about through altered surface wind stress attributable to a change in topography, or through increases in deep-water production, perhaps associated with ocean-sill changes. Raymo noted that there is now some evidence that North Atlantic Deep Water production was greater during the late Pliocene[9].

Where does this leave us? The participants generally agreed that although gradual uplift undoubtedly occurred in some regions, perhaps leading to increased erosion, the effects of these processes on climate are still debatable. We do not know what the CO_2 levels were in the Tertiary, nor whether higher CO_2 was in fact responsible for the warmth of those times. The question of the applicability of Tertiary climates as analogues for future trace gas-induced warming remains an open one. □

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EVOLUTIONARY BIOLOGY

What the sperm count costs

Linda Partridge and Paul H. Harvey

DISSECTING the sex life of the nematode worm *Caenorhabditis elegans* has already provided surprises for biologists interested in life-history theory. In a report on page 456 of this issue[1], Van Voorhies throws another spanner in the works by demonstrating that the costs of producing sperm are not as negligible as we might have thought.

C. elegans individuals are normally self-fertilizing hermaphrodites, although the occasional male crops up from time to time. Last year's big surprise was that individual hermaphrodites usually produce more eggs than sperm, and that fecundity is limited by sperm production[2]. Mutants that produced more sperm and fewer eggs left more offspring during their lifetime. The reason such mutants are selected against is that sperm are produced before eggs, so that the generation time for an individual that produces fewer sperm is shorter. In a growing population, which is where a reproducing *C. elegans* is likely to find itself, short generation time can be favoured over higher lifetime fecundity, and so the wild type can win against the more fecund mutants[2,3]. Van Voorhies also uses mutants that are expected to change life-history schedules in predictable ways, and then sees if they do.

Sex differences

Biologists, who usually define males and females by the relative size of their gametes, believe that many other sex differences follow from this fundamental one. The argument generally runs along the following lines. If we assume that males and females have roughly the same amount of resources to devote to gamete production, then males will be able to produce more gametes than females. Now make the further assumption that gametes are the only resources donated to the offspring, and it follows that female gametes will become a limiting resource for male reproduction. Males should compete to gain access for their sperm (or pollen) to eggs (or ovules)[4]. Such competition among males has led to the sexual selection of characters producing high male mating success, and hence the elaborate ornamentation and weaponry of the males of many species[5].

Resources devoted to reproduction cannot be used for other vital processes, such as repair and maintenance, which are important for survival. Van Voorhies' experiments use decreases in rates of survival, or lifespan, to compare the costs of reproduction for both males and females. It is well established that such costs of reproduction can be important in practice[6]. If eggs are more expensive to produce than sperm, when a fixed number of eggs is added to a clutch we should expect to see a greater drop in survival for the female than for a male adding the same number of sperm. When hermaphrodites were mated to males (hermaphrodites will not mate with each other), the egg output went up two to threefold, yet lifespan in the mated hermaphrodites was no lower than that of unmated controls. In contrast, mating did reduce the lifespan of males and it is also known to increase their sperm production. Further evidence that the cost of mating was a consequence of making sperm, rather than the physical act of copulation, came from the finding that lifespan was increased relative to wildtype controls in both males and hermaphrodites that carried a mutant making them defective in spermatogenesis.

In the face of this evidence, the conclusion that each sperm costs more than each egg may seem hard to resist. However, males produce far more sperm (3,000+) than are needed to fertilize a hermaphrodite's eggs. Perhaps some of those sperm are metabolized into eggs after a hermaphrodite mates, thereby reducing the apparent cost of egg production. Nevertheless, high costs of spermatogenesis seem inescapable. Costs of reproduction for males are not new[7], but the finding that spermatogenesis can so effectively curtail survival certainly is. On the basis of the data from the males alone, it could be argued that males are different from hermaphrodites in respects other than gamete production, and they also produce more sperm, and that is why males show such large reproductive costs.

Limiting factors

Sperm are qualitatively as well as quantitatively different from eggs, which may help explain why they are so costly to produce. Some support for this idea comes from a comparison of the rates of oogenesis versus spermatogenesis in *C. elegans*. Instead of the 1:500 ratio predicted by the size difference, sperm volume is produced at only 12.5 times the rate of egg volume. Sperm may contain a limiting nutrient that is present in larger quantities than in eggs, their synthesis may require more energy, or the rate of meiosis may be limiting. Whatever the explanation, *C. elegans* sperm are clearly limiting for female reproduction, contrary to the general expectation. Under such circumstances, hermaphrodites would be expected to compete for matings with males. Van Voorhies' unexplained finding that the act of mating itself appears to increase male lifespan would select further for a more than usually sex-mad male phenotype. Indeed, we are left wondering why selection has not succeeded in producing more males. □

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